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Searching for the Neural Correlates of Object Priming

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"Object priming" is characterized by increased efficiency in identifying an object as a result of prior exposure to that object. A particularly striking example of this form of implicit learning comes from object-naming studies: Previously named object pictures are named faster than novel object pictures. This facilitation of naming speed is extremely long-lasting (up to 48 weeks, the longest interval tested; Cave, 1997). Amnesic patients show normal levels of object name priming with up to a week intervening between repetitions (Cave & Squire, 1992). These findings suggest that naming an object produces a more or less permanent change in processing efficiency, and that the development of this change is not dependent on the medial temporal lobe memory system.

Functional brain imaging has revealed that this seemingly simple act of naming an object is mediated by a hierarchically organized, interactive network of discrete cortical regions (Bouchart et al., 2000; Martin, Wiggs, Ungerleider, & Haxby, 1996). This network typically includes bilateral regions of occipital, temporal, left inferior frontal cortices and the left insula. Activity in these regions reflects different component processes necessary for object naming, including visual processing of the physical stimulus, and retrieval of semantic, lexical, and phonological representations (for reviews, see Martin, 2001; Martin & Chao, 2001; and Price, Indefrey, & van Turennout, 1999). In this chapter, we highlight our recent experiments that have explored the association between object priming and changes in neural activity in different regions of the object-naming system.

DECREASED ACTIVITY IN POSTERIOR CORTEX: CREATION OF SPARSER YET MORE OBJECT-SPECIFIC REPRESENTATIONS

In 1992, Squire and colleagues (1992) used positron emission tomography (PET) to record regional cerebral activity while subjects generated words to three-letter word stems. Completing the stems with previously studied words resulted in less neural activity in occipital

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cortex (right lingual gyrus), compared with generating words to stems that could not be completed with previously studied words (Squire et al., 1992). Following this report, decreased neural activity with repetition of words, as well as objects, was found in studies using PET (Buckner et al., 1995; Schacter, Alpert, Savage, Rauch, & Albert, 1996) and functional magnetic resonance imaging (fMRI) (Buckner et al., 1998; Buckner, Koutstaal, Schacter, & Rosen, 2000; Martin et al., 1995; Wagner, Maril, & Schacter, 2000). Moreover, decreases, though commonly including occipital cortex, were not limited to this region, but rather tended to include most of the cortical regions engaged by the task (for reviews, see Schacter & Buckner, 1998; Wiggs & Martin, 1998).

An early demonstration of this phenomenon using fMRI can be seen in Figure 19.1. Subjects were scanned while silently naming pictures of objects. The first block of trials consisted of pictures that the subjects had not previously seen. This block was followed approximately 30 seconds later by a repetition of these pictures in a different order, followed by another set of novel object pictures. Interspersed between these object blocks were series of visual noise stimuli that subjects were told to stare at, and that served as a baseline condition (Martin et al., 1995). As illustrated by Figure 19.1, relative to the visual noise baseline, silent object naming produced a robust response that was significantly decreased when the same objects were again named, and then returned to its initial level of
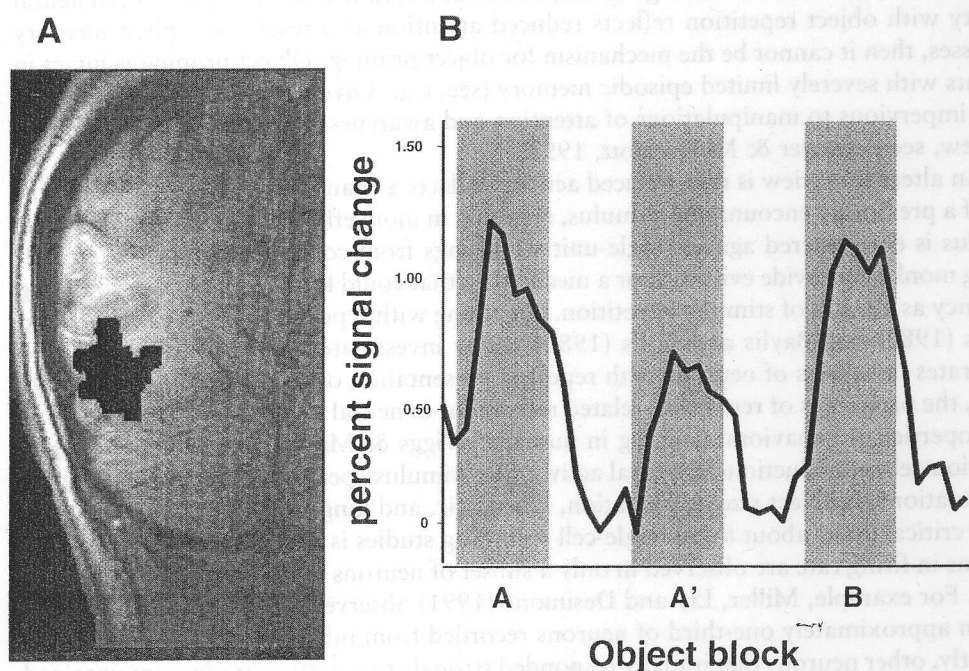
FIGURE 19.1. (A) Coronal section of the left hemisphere of a single subject. Shown is a region in the posterior temporal cortex (black) that was more active during silent object naming relative to viewing noise patterns. Recording was made with a surface coil place along the left side of the subject's head. (B) fMRI time series showing how activity in this region was modulated by silent naming of a series of novel objects (A), repeated presentation of these novel objects (A'), and a new set of objects (B). Data were averaged across all active voxels in the region and across six runs of the A-A'-B series. Different objects were presented in each run. Alternating blocks of object (gray bars) and visual noise (white bars) lasted 21 seconds. Data from Martin et al. (1995).

activity when new objects were presented. These and similar findings (Buckner et al., 1998) suggested that fMRI could be used to investigate modulation of neural activity across different regions of the cortex within a relatively short time frame.

As Squire and colleagues (1992) noted in their original report, two types of explanations could account for priming-related reductions in neural activity. One possibility is that they reflect changes in the processing demands of the task. For example, in the Squire and colleagues report, subjects may have recognized that the stems were beginnings of words they had recently studied, thereby requiring less attention than the novel word stems presented during the baseline condition. Indeed, when subjects were explicitly instructed to complete stems with recently studied words, reduced activity was again noted, albeit to a lesser extent than in the priming condition (Squire et al., 1992). A similar explanation could be offered for the fMRI time series illustrated in Figure 19.1. In this study, novel and repeated objects were presented in sequential blocks. As a result, it could be argued that subjects quickly became aware of this sequence, resulting in less attention devoted to the repeated objects, and a corresponding reduction in neural activity. Thus, within this framework, priming-related reductions in neural activity reflect changes in attention as a consequence of explicit memory of the recent past.

Modulation of the fMRI signal by attentional task demands is certainly of interest. Indeed, many studies have shown that selective attention can either suppress or enhance neural activity (see Kastner & Ungerleider, 2000, for a review). However, if reduced neural activity with object repetition reflects reduced attention as a result of explicit memory processes, then it cannot be the mechanism for object priming. Object priming is intact in patients with severely limited episodic memory (see, e.g., Cave & Squire, 1992) and relatively impervious to manipulations of attention and awareness in normal individuals (for a review, see Roediger & McDermott, 1993).

An alternative view is that reduced activity reflects a change in the neural representation of a previously encountered stimulus, resulting in more efficient processing when that stimulus is encountered again. Single-unit recordings from cortical neurons in alert, behaving monkeys provide evidence for a mechanism that could lead to enhanced processing efficiency as a result of stimulus repetition. Beginning with reports by Brown, Wilson, and Riches (1987) and Baylis and Rolls (1987), many investigators have observed reduced firing rates in subsets of neurons with repeated presentation of stimuli. As reviewed elsewhere, the properties of repetition-related reductions in neural firing rates mirror many of the properties of behavioral priming in humans (Wiggs & Martin, 1998). For example, repetition-related reductions in neural activity are stimulus-specific, graded, unaffected by manipulations of object size and location, automatic, and long-lasting.

A critical point about these single-cell recording studies is that repetition-induced reductions in firing rate are observed in only a subset of neurons that initially respond to an object. For example, Miller, Li, and Desimone (1991) observed repetition-related reductions in approximately one-third of neurons recorded from inferior temporal cortex. Importantly, other neurons that initially responded strongly to a particular object maintained their firing rate with subsequent object repetitions. As suggested by Desimone (1996), this stimulus-specific pattern of maintained response in some neurons, coupled with reduced response in others, might provide a mechanism for repetition priming. Specifically, as object-specific features are learned through experience, neurons strongly tuned to these features maintain their firing rates, whereas neurons less strongly tuned gradually drop out of the responsive pool. As a result, repeated exposure to an object leads to a sparser and yet more object-specific representation, which in turn results in enhanced object identification. Thus, within this view, facilitation of performance in priming tasks does not result specifically

from reduced attentional demands, but rather from the formation of sparser yet more stimulus-specific representations, leading to more efficient stimulus processing.

In a recent experiment (van Turennout, Ellmore, & Martin, 2000), we sought to tighten the link between the reduced neural activity and the sparse representation view by using a design that should greatly reduce, if not eliminate, changes in attentional demands for processing novel versus repeated objects. In addition, we sought to determine whether repetition-related reductions as measured by fMRI would extend to two characteristics of behavioral priming. First, reductions should occur regardless of whether the object has a preexisting representation in memory (see, e.g., Gabrieli, Milberg, Keane, & Corkin, 1990; Schacter, Cooper, & Delaney, 1990). Second, they should be long-lasting. As mentioned previously, behavioral studies report object priming using a naming task with lags of nearly a year (Cave, 1997), suggesting a permanent change in processing efficiency that can be established after a single experience.

In our study, we took advantage of a relatively new development in fMRI methodology: event-related designs (Buckner et al., 1998; D'Esposito, Zarahn, & Aguirre, 1999). In contrast to presenting stimuli blocked by condition, event-related designs allow different types of stimuli or conditions to occur in a randomly intermixed order. As a result, subjects are unable to anticipate the next stimulus event, and thus are discouraged from developing strategies that could confound the interpretation of the results.

Several days prior to the scanning session, subjects engaged in an object-naming task. Each object was presented for 200 milliseconds (msec) at a rate of one item every 2 seconds. Interspersed between the pictures of real objects that the subjects named aloud were pictures of nonsense objects. Subjects were instructed to attend carefully to each object, even if they could not name it. Three days later, subjects participated in the scanning session. Again, objects were presented as in the prior training session. Subjects were told to name each object silently, and to look carefully at the nonsense objects. During scanning, subjects saw real objects and nonsense objects that had been presented previously, objects and nonsense objects that they had not previously seen, and repetitions of these novel objects after a delay of approximately 30 seconds. In addition, visual noise stimuli were included to provide a low-level baseline (van Turennout et al., 2000). Presentation of these seven stimulus types in a random, intermixed order, with items appearing for only 200 msec, made it highly unlikely that a reduced neural response associated with object repetition would result from reduced attentional demands for processing repeated versus novel objects.

Relative to naming new objects, neural activity in posterior cortex was markedly reduced when objects were repeated after a 30-second delay. Moreover, reduced activity was present, although to a weaker extent, after a 3-day lag (see Figure 19.2; see also Wagner et al., 2000, for reduced neural activity in a word-priming task after a 1-day lag). These findings mirrored the behavioral data collected outside the scanner with a different group of subjects. Object-naming speed was strongly facilitated at the short delay, and to a lesser extent at the longer delay.

The same pattern of results was found for viewing nonsense objects. Repetition of nonsense objects was associated with a robust reduction in neural activity after a 30-second delay. Relative to viewing nonsense objects for the first time, activity was also reduced for nonsense objects presented 3 days earlier. These reductions tended to be confined to occipital cortex, whereas the reductions extended into the posterior region of ventral temporal cortex for real objects (see van Turennout et al., 2000, for details). Thus a single, brief (200-msec) presentation of an object can lead to long-term changes in neural activity, even when that object has no prior representation in memory.

A. Real objects

B. Nonsense objects
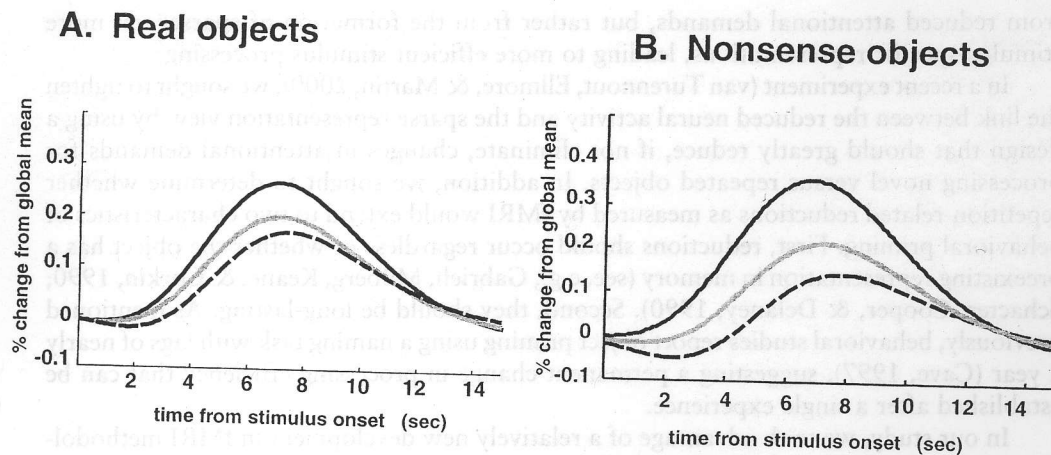
FIGURE 19.2. (A) Fitted responses for novel real objects (black), repeated objects at a 30-second delay (dashed line), and repeated objects at a 3-day delay (gray). Shown are group-averaged event-related hemodynamic responses computed from all voxels within the left occipitotemporal cortex active during object naming, showing an effect of object repetition. (B) Same as in A, but showing an effect in occipital cortex for viewing nonsense objects (see the original paper for details). Data from van Turennout, Ellmore, and Martin (2000).

These findings are consistent with the idea that behavioral priming is attributable to changes in object representations stored in posterior cortex. In addition, they cast doubt on the usefulness of explanations of priming-related neural reductions that appeal solely to changes in attention or other processing strategies. However, additional findings from this study indicate that no single mechanism is likely to account fully for neural changes associated with object priming in naming tasks.

INCREASED ACTIVITY IN THE INSULAR CORTEX: A FORM OF PROCEDURAL LEARNING?

In the van Turennout and colleagues (2000) study, silently naming objects produced increased activity in left inferior frontal cortex (Broca's area) and the anterior region of the left insula, as is typically seen during object naming and other language tasks (Martin et al., 1996; Price, Moore, Humphreys, Frackowiak, & Friston, 1996). However, repetition-related changes in these anterior sites were in stark contrast to those seen in posterior cortical regions. Whereas decreases were stronger at the short (30-second) than at the long (3-day) delay in posterior cortex, activity in Broca's area showed a minimal decrease after 30 seconds and a large decrease when 3 days intervened between the first and second object presentations. Moreover, whereas activity in Broca's area declined as a function of delay, the left anterior insula showed the opposite pattern: Activity was minimal when objects were first named, increased in response to objects repeated after 30 seconds, and increased further when naming objects that were first seen 3 days prior to the scan session (Figure 19.3). (Neither the insula nor Broca's area was active for viewing nonsense objects.)

These findings have been replicated and extended in a more recent event-related study that investigated the time course of these changes in greater detail (van Turennout, Biela-mowicz, Ellmore, & Martin, 2001). Again, activity in Broca's area decreased and activity

A. Left inferior frontal

B. Left insula
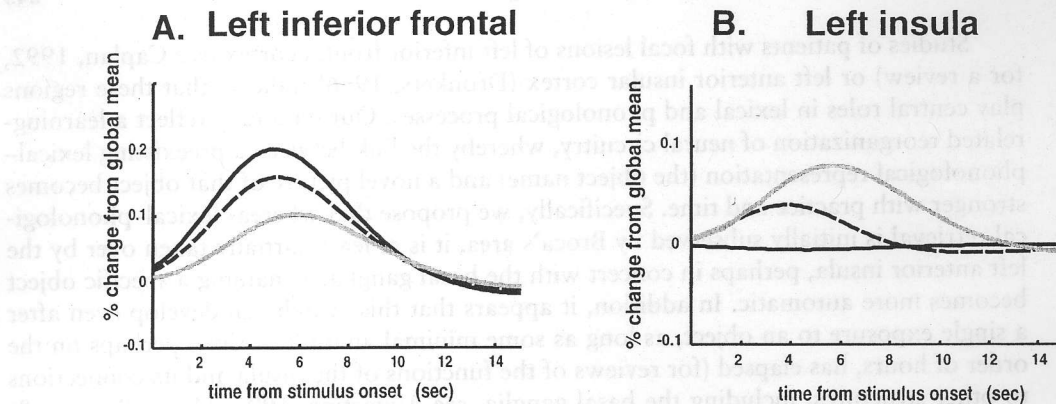
FIGURE 19.3. (A) Fitted responses for novel real objects (black), repeated objects at a 30-second delay (dashed line), and repeated objects at a 3-day delay (gray). Shown are group-averaged event-related hemodynamic responses computed from all voxels within the left inferior frontal cortex active during object naming, showing an effect of object repetition. (B) Same as in A, but for the left insular cortex (see the original paper for details). Data from van Turennout, Ellmore, and Martin (2000).

in the insula increased, with repetition lags that now included 1 hour, 6 hours, and 3 days. An added feature of this study was that a set of novel objects were repeated multiple times during scanning (three repetitions at approximately 30-second intervals). For these objects, the same contrasting patterns of activity in Broca's area and the insula were observed: Activity decreased in Broca's region and increased in the left insula as objects were named repeatedly. In addition, increased activity with repeated practice was found in the left basal ganglia.

To what can we attribute these complex patterns of response? Clearly, the increased activity in the insular cortex is at odds with both the attention and sparse encoding hypotheses. Both of these ideas would predict the greatest amount of activity to novel objects, which would then decrease with repetition. An alternative possibility is that this increased activity reflects explicit remembering. Activity may be increasing with repetition because subjects are becoming more and more aware of having seen the object previously. This explanation, however, is not supported by the data for objects repeated only once at different time lags. Subjects should be more aware, and thus insular activity should be greater, for objects repeated after short delays than after long delays. Yet the opposite pattern of activation was found.

Another alternative is that the increased activation in the anterior insula, coupled with decreased activity in Broca's area, reflects a form of procedural learning whereby performance becomes more automatic with practice. This idea was first proposed by Raichle and colleagues (1994) to account for the practice-related changes in verb generation. As subjects continued to generate the same verb in response to the same noun, activity increased in insular cortex bilaterally (and in left medial occipital cortex), and decreased in left inferior frontal cortex (and in left posterior temporal cortex, left anterior cingulate, and right cerebellum). These changes were reversed when new nouns were presented, suggesting a change in neural circuitry as task performance became more automatic (see Petersen, van Mier, Fiez, & Raichle, 1998, and Raichle, 1998, for additional findings and extended discussion).

Studies of patients with focal lesions of left inferior frontal cortex (see Caplan, 1992, for a review) or left anterior insular cortex (Dronkers, 1996) indicate that these regions play central roles in lexical and phonological processes. Our data may reflect a learning-related reorganization of neural circuitry, whereby the link between a preexisting lexical–phonological representation (the object name) and a novel picture of that object becomes stronger with practice and time. Specifically, we propose that whereas lexical–phonological retrieval is initially subserved by Broca's area, it is at least partially taken over by the left anterior insula, perhaps in concert with the basal ganglia, as naming a specific object becomes more automatic. In addition, it appears that this switch can develop even after a single exposure to an object, as long as some minimal amount of time, perhaps on the order of hours, has elapsed (for reviews of the functions of the insula and its connections to other structures, including the basal ganglia, see Augustine, 1996; Flynn, Benson, & Ardila, 1999).

CONCLUSIONS AND FUTURE DIRECTIONS

These findings have a number of implications for understanding the functional neuroanatomy of memory systems in the brain. First, changes in neural activity occur automatically with object repetition. These changes reflect the object's presentation history and the brain's response to it, not reduced attentional demands resulting from remembering that history. Second, the data suggest that object name priming is mediated by two distinct mechanisms. The first mechanism is the formation of a sparser yet more object-specific representation, yielding enhanced object identification. This view is consistent with models viewing priming as a change in presemantic, perceptual representational systems that results in improved recognition (Tulving & Schacter, 1990). Single-unit recordings from monkey cortex suggest that the neural correlates of this process are a progressive decline in the firing rate of a subset of neurons that initially responded to the object, coupled with the continued firing of neurons that code the critical features necessary to identify that object (Desimone, 1996; Wiggs & Martin, 1998; see also Rolls & Tovee, 1995, for a discussion of the role of sparse encoding in object recognition). Because the fMRI signal reveals the aggregate activity of large populations of neurons, this process is reflected as a signal reduction (but see James, Humphrey, Gati, Menon, & Goodale, 2000, for a different interpretation of repetition-related reductions measured by fMRI).

The second mechanism may be a form of procedural learning characterized by increased efficiency in name retrieval in response to a specific object picture. This view is consistent with the idea that object name priming results from facilitation in the linking of an object's features and its associated phonological representation (Wheeldon & Monsell, 1992). The neural correlates of this process appear to be a progressive decline in activity in Broca's area, coupled with a progressive increase in activity in the left insula and basal ganglia. It remains to be determined whether patients with lesions of the left insula or basal ganglia show impaired object name priming, especially with long delays between presentations. The present data suggest that this pattern of results should be observed.

Clearly, many questions remain concerning the neural correlates of object priming. The most common feature reported across studies is a repetition-related decrease in posterior cortical activity. However, there is no universal agreement on the interpretation of this effect (see, e.g., James et al., 2000). Moreover, contrary to our findings with nonsense objects, object repetition-related *increases* in posterior cortex have been reported in studies

using novel stimuli (Henson, Shallice, & Dolan, 2000; Schacter et al., 1995). Much work is needed to characterize the effects that different stimulus characteristics (e.g., familiarity) and priming paradigms have on repetition-related changes in neural activity. Finally, we have argued throughout this chapter that these neural changes reflect implicit memory phenomena (priming and procedural learning). Nevertheless, subjects are perfectly capable of explicitly recognizing objects they have previously named. In fact, object recognition memory can remain above chance levels even after nearly a year has elapsed between presentations (Cave, 1997). How the changes described here interact with explicit memory processes (Wagner et al., 2000) remains to be determined.

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